is with the chinchilla (C^{ch}) allele at the albino locus of the house mouse[3]. This allele in the house mouse has a much more pronounced effect on phaeomelanin than eumelanin so that in agouti mice the subapical yellow band is much lighter. Since chinchilla has no influence on the length of the pigmented regions of agouti hairs in the house mouse while the gray mutation in spiny mice shows an extension of the black pigment further down the spine, this homology seems less likely. A further alternate hypothesis, that the mutation is at the extension locus, also is less likely since mutations at the extension locus that extend black pigment are generally dominant alleles[5,6]. On the basis of the available data it is not possible to be sure of the genetic homology. The mutation also could be interfering with the normal process of coat maturation, thus maintaining the juvenile coat color, even though it is not a mutation at a coat-color locus.

This mutation seems to involve coat color only. There do not appear to be any other differences between wild-type and gray animals. However, if metabolic or behavioral changes are associated with the mutation it will be difficult to study them. The spiny mouse is not an ideal species for genetic research because it has a small litter size (1–6) and a relatively long gestation (38 days)[2]. Also, the best breeding pairs are established before the animals are sexually mature. Matings established after the animals are sexually mature are not very successful. In most cases the adult animals are very aggressive towards strange animals. This makes it difficult to establish desired matings and to make test matings of one female to males of both phenotypes.

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Inheritance of resistance to blackeye cowpea mosaic and cowpea aphid-borne mosaic viruses in *Phaseolus vulgaris*

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ABSTRACT: In populations from crosses of resistant and susceptible plants of the bean (*Phaseolus vulgaris*) cultivar Black Turtle Soup, resistance to blackeye cowpea mosaic virus (BlCMV) and to cowpea aphid-borne mosaic virus (CAbMV) was conferred independently by single dominant factors that appear to be closely linked. The symbol *Bcm* was assigned to the gene for BlCMV resistance and *Cam* to that for CAbMV. Linkage was determined by separately inoculating plants of the testcross with both viruses on different leaves. Since BlCMV and CAbMV incite identical symptoms, but do not cross protect against each other, their presence in each susceptible plant was determined by enzyme-linked immunosorbent assay (ELISA). This detection method was highly specific because the two viruses are distantly related serologically. The normally resistant plants responded with a lethal systemic hypersensitive reaction when approach-grafted to BlCMV- or CAbMV-infected plants, or when mechanically inoculated and held constantly at 35°C.

RECENTLY we reported that blackeye cowpea mosaic virus (BlCMV) and cowpea aphid-borne mosaic virus (CAbMV) are distantly related serologically, do not cross protect against each other, and resistance to them in cowpea (*Vigna unguiculata* (L.) Walp.) is conferred by distinct genetic factors[7–9]. Thus, it was concluded that these viruses are two distinct members of the potyvirus group[4,8,9]. However, BlCMV and CAbMV share some common features, such as the length of virus particle, size of capsid protein, and sedimentation rate of nucleic acid[9]. In addition, bean cultivars resistant or susceptible to one of these viruses also are resistant or susceptible to the other[9]. In susceptible bean genotypes the symptoms incited by BlCMV or CAbMV are strikingly similar.

The aim of this study was to determine the mode of inheritance and the nature of resistance to BlCMV and CAbMV in identical genetic populations of a cultivar of *Phaseolus vulgaris* L., and to define the relationship between the resistance factors.

Materials and Methods

Genetic populations were derived from crosses between two selections of the same bean cultivar, Black Turtle Soup. Black Turtle 1 (BT1) is resistant to BlCMV and CAbMV, whereas Black Turtle 2 (BT2) is susceptible to both viruses. These two lines have been used in genetic studies involving other viruses[5,6].

To determine the mode of inheritance of resistance, plants of BT1, BT2, and their F_1, F_2, and reciprocal backcross generations were inoculated with the Florida isolate of BlCMV (BlCMV-Fla)[9] and the Moroccan isolate of CAbMV (CAbMV-Mor)[4,9]. Inocula for mechanical transmissions were prepared from leaves of cowpea plants infected with either of these two viruses. Foliar tissue was homogenized with phosphate buffer (K^+) (pH 7.4) and extracts were rubbed onto primary leaves of bean plants that had been dusted with 400 mesh carborundum. To minimize escapes among susceptible genotypes, plants were reinoculated a week later on the first trifoliolates. All plants, regardless of their reaction to the viruses, were assayed for both BlCMV and CAbMV by the enzyme-linked immunosorbent assay (ELISA) method, as originally described by Clark and Adams[2] and modified by Taiwo and Gonsalves[8]. Antiserum to BlCMV-Fla and to CAbMV-Mor had been prepared by Taiwo and Gonsalves[8].

To determine the nature of resistance in resistant BT1 plants, they were approach-grafted to BT2 plants, which were then inoculated with BlCMV or CAbMV.

For linkage determination between factors for resistance to BlCMV and CAbMV, each plant of the testcross was inoculated separately with these viruses, one virus on each primary leaf. Since preliminary studies indicated that the incubation period in susceptible BT2 plants at 25°C is 5–6 days for BlCMV and 7–8 days for CAbMV, inoculations with BlCMV were delayed about 60 hours after leaves were inoculated with CAbMV. The local and systemic presence of these two viruses was ascertained by ELISA tests. Each plant was assayed for both viruses using tissue from inoculated (local infection) and noninoculated trifoliates (systemic infection). All the experiments were conducted in an insect-free greenhouse maintained at 25°C.

Results

Reaction of parents. Plants of the resistant parent BT1 inoculated with BlCMV or CAbMV remained free of local and systemic infection. Plants of the susceptible parent, BT2, reacted similarly to both viruses. Symptoms included leaf epinasty, local chlorotic spots, and a severe systemic mottle and distortion. Plant growth was considerably reduced, older leaves became chlorotic and abscised prematurely and no pods were produced. The reaction of BT1 plants that had been approach-grafted to BT2 plants inoculated with BlCMV or CAbMV, was lethal. Within 15 days of inoculation, all BT1 plants had developed apical and stem necrosis followed by death. Identical reactions were noted in plants of BT1 when they were mechanically inoculated with BlCMV or CAbMV and incubated constantly at 35°C.

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Reaction of breeding lines. Plants of (BT1 × BT2)F_1 inoculated with BlCMV or CAbMV remained free of symptoms and assays revealed the absence of local and systemic infections. However, when these plants were approach-grafted to infected BT2 plants, they collapsed with apical and stem necrosis. Plants of the F_2 generation segregated closely to the ratio of 1 susceptible to 3 resistant to BlCMV (Table I) and to CAbMV (Table II). A few resistant plants occasionally developed some local veinal necrosis, which in two plants progressed to cause apical necrosis and later death. Plants of the backcross (BT1 × BT2) × BT1 remained free of local and systemic infection with both viruses. Plants of the testcross (BT1 × BT2) × BT2 segregated approximately to the ratio 1 resistant to 1 susceptible. From the data presented in Tables I and II, it is concluded that resistance to BlCMV or CAbMV is conditioned by single dominant factors.

Linkage between resistance factors. Following inoculation with BlCMV and CAbMV, all plants of the testcross population segregated into two classes, resistant or susceptible. In each susceptible plant, the local and systemic presence of these viruses was demonstrated by ELISA tests. The data presented in Table III clearly indicate that the gene for resistance to BlCMV and that for CAbMV are closely linked.

Discussion

Similarities in mode of inheritance, nature of resistance, and an apparent close linkage between resistant factors, suggest a common gene for resistance to BlCMV and CAbMV in the bean line BT1. However, until an analysis of nucleotide sequence homologies of these two viruses and the resistance genes of BT1 becomes available, it is prudent to consider the two factors for resistance as independent entities. Thus, the symbol *Bcm* (Blackeye cowpea mosaic) is assigned to the single dominant factor for resistance to BlCMV, and *Cam* (Cowpea aphid-borne mosaic) to that conferring resistance to CAbMV.

The use of the same plants of the testcross to determine linkage between *Bcm* and *Cam* was possible because of the lack of cross protection and the absence of a close serological relationship between BlCMV and CaBMV[4,8,9]. Distant or intermediate serological relationships among some viruses are usually not detected with ELISA[3]. The lack of cross reactivity with the ELISA system between BlCMV-Fla and CAbMV-Mor was noted by Taiwo and Gonsalves[8], and exploited in this work. Using ELISA, it was established that each plant of the testcross was either resistant or susceptible to both viruses. The difference in incubation periods was easily overcome by delaying inoculations with BlCMV, the virus having the shorter incubation period. The combined effect of both viruses in susceptible genotypes was no more severe than the symptoms incited by each virus separately.

The systemic hypersensitive reaction in plants of BT1 when graft-inoculated or mechanically inoculated with BlCMV or CAbMV and incubated at high temperature is known to occur with other viruses[5].

For BlCMV as well as CAbMV, seed transmission in cowpea represents the major source of inoculum[1,10]. However, no information is available regarding the seedborne nature of BlCMV or CAbMV in seed of susceptible bean genotypes, because the severity of symptoms usually causes premature death of infected plants. Data are not available concerning the natural occurrence of these two viruses in bean crops. But, if a susceptible cultivar is grown in the vicinity of a BlCMV or CAbMV infected cowpea field, conceivably the viruses could spread to the bean plants with devastating consequences. Both of these viruses are readily spread by a number of aphid species in a stylet-borne manner[1,10].

Some of the bean lines currently used as sources of resistance to root-rot pathogens (PI 109859, PI 165435, PI 203598, PI 203958, and others) were determined to be susceptible to BlCMV and CAbMV, consequently adequate testing of breeding lines deriving from these plant introductions is recommended. However, it is reassuring to know that the majority of the leading commercial bean cultivars possess resistance to BlCMV and CAbMV[9].

Table I. Segregation ratios of cross and backcross populations of *Phaseolus vulgaris* Black Turtle 1 (BT1) with Black Turtle 2 (BT2) for resistance to blackeye cowpea mosaic virus

Populations	No. plants* R	S	Exp. ratio	Goodness-of-fit (*P*)
BT1	110	0		
BT2	0	129		
(BT1 × BT2)F_1	46	0		
BT1 × BT2)F_2	184	54	3:1	0.43
(BT1 × BT2)F_1 × BT1	78	0		
(BT1 × BT2)F_1 × BT2	54	49	1:1	0.62

* R = resistant; S = susceptible

Table II. Segregation ratios of cross and backcross populations of *Phaseolus vulgaris* Black Turtle 1 (BT1) with Black Turtle 2 (BT2) for resistance to cowpea aphid-borne mosaic virus

Populations	No. plants R	S	Exp. ratio	Goodness-of-fit (*P*)
BT1	106	0		
BT2	0	117		
(BT1 × BT2)F_1	49	0		
(BT1 × BT2)F_2	214	68	3:1	0.74
(BT1 × BT2)F_1 × BT1	95	0		
(BT1 × BT2)F_1 × BT2	54	49	1:1	0.62

Table III. Reaction of testcross plants of *Phaseolus vulgaris* Black Turtle 1 (BT1) with Black Turtle 2 (BT2), when inoculated with blackeye cowpea mosaic virus (BlCMV) and cowpea aphid-borne mosaic virus (CAbMV) on different leaves. Both viruses were detected locally and systemically by enzyme-linked immunosorbent assay (ELISA) in each susceptible plant

Population	Virus	No. plants R*	S†	Exp. ratio	Goodness-of-fit (*P*)
(BT1 × BT2) × BT2	BlCMV	54	49	1:1	0.62
	CAbMV	54	49		

* Plants resistant to BlCMV also were resistant to CaBMV
† Plants susceptible to BlCMV also were susceptible to CaBMV

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